BIOLOGICAL RELATIONS OF DESERT SHRUBS.

II. ABSORPTION OF WATER BY LEAVES.

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DURING a study of certain shrubs growing in the vicinity of the Desert Botanical Laboratory near Tucson, Arizona, it has been found that the leaves of some of them absorb water, while those of others do not. Although leaf absorption is treated by leading physiologists as a matter of indifference, or at any rate of secondary importance, it has seemed worth while to inquire whether differences of habit in this particular, on the part of these desert plants, may not be correlated with other characteristic peculiarities; if so, even if the fact should turn out to be of small importance physiologically, it may be significant from a biological point of view.

Our knowledge of leaf absorption as yet is fragmentary and uncertain. For the general subject it is quite unnecessary to cite the voluminous and contradictory literature. DANDENO[1] has given a useful historical résumé, reference to which and to paragraphs in BURGERSTEIN'S more recent work[2] is sufficient for the present purpose. In regard to various highly modified plants, however, the case is quite different. SCHIMPER has made such detailed observations of certain epiphytes as to leave no doubt that they normally absorb large quantities of water through their aerial parts, and that this is a distinct physiological advantage, or even necessity. In view also of investigations cited by BURGENSTEIN it becomes necessary to accept the fact of leaf absorption in the case of various other plants.

As for the plants of arid regions, the evidence has been less conclusive than could be wished. VOLKENS, in his classical work, describes various special structures by means of which, presumably, many of the plants of the Egyptian-Arabian desert take up dew

[1] DANDENO, J. B. An investigation into the effects of water and aqueous solutions of some of the common inorganic substances on foliage leaves. Trans. Can. Inst. **7**:238. 1901.

[2] BURGERSTEIN, A., Die Transpiration der Pflanzen. 1904.

through their leaves, but the woody species growing in the arid territory of the southwestern United States are so different in their habits and in their environmental relations as to preclude the settlement of the question for them, even within the bounds of probability, in any other way than by direct observation and experiment; in fact they are found, as regards leaf absorption, to differ widely among themselves. The object of the present paper, therefore, is the presentation of such facts as have been determined for a limited number of species indigenous to southern Arizona.

In this region existing physical conditions give to the question special interest. As is well known, precipitation is meager, except at relatively high altitudes, and is distributed throughout the year, with no distinctively rainy season. The rainfall, moreover, is extremely uncertain, and for months at a time is often so slight that it does not wet the soil for more than a few centimeters, an amount of precipitation likely to be of very little positive advantage as far as root absorption is concerned. Under such circumstances, in which delicate adjustment is the condition of survival, it would seem that plants capable of leaf absorption might have a distinct advantage in times of prolonged drouth, during which occasional showers occur which are too light to penetrate the soil. As will be seen, however, only a limited number of species appear to enjoy this advantage to an appreciable extent.

Nearly all of the species selected for investigation grow in the immediate vicinity of the Desert Laboratory. A single one, *Holacantha Emoryi*, which seems not to be indigenous here, was obtained from the grounds of the University of Arizona. The following classification of the plants employed into biological groups is provisional, but will serve to direct attention to the very diverse ecological history of the species now growing together in this region.

BIOLOGICAL CLASSIFICATION OF PLANTS STUDIED.

I. Shrubs, with relatively slight modification of form and structure, their habits plainly indicating mesophytic origin. Celtis, Covillea, Lycium.

II. Shrubs or small trees, more conspicuously modified, but retaining manifest traces of mesophytic habits. Parkinsonia, Prosopis, Acacia.

III. Woody or partly herbaceous plants, exhibiting peculiar modifications of distinctly xerophytic types. Fouquieria, Holacantha, Koerberlinia, Zizyphus, Atriplex.

IV. Plants of the most pronounced xerophytic character. Opuntia, Cereus, and other cacti.

V. Plants adapted by habit, rather than structure, to desert conditions. Sphaeralcea and many other half-shrubby or more or less herbaceous forms.

Of the species employed in the experiments, *Celtis pallida* is a shrub, growing commonly to the height of one to one and one-half meters on the laboratory hill, where it is rather abundant. It holds its foliage so well that it might be ranked as an evergreen, though it suffers to some extent from the effects of frost. Its leaves are rough-hairy, thin but firm in texture, and conforming in general to the generic type. *Covillea tridentata*, the well-known creosote bush, is the most abundant woody species of this region. Its small coriaceous leaves, presented more or less edgewise to the sun and covered with waxy varnish, are well protected against excessive transpiration. *Lycium Berlandieri* is a small shrub, more than a meter in height, of frequent occurrence on rocky exposures. These species, of the three genera named, while well adapted to their habitat, exhibit characters far less conspicuously xerophytic than those of many of the plants with which they are associated.

Coming to the second group, *Parkinsonia Torreyana* attains the dimensions of a small tree, and is conspicuous by reason of its green bark, from which it has the common name of *palo verde*. Though a denizen of the desert, it is not a dry ground form, but frequents low places, where more water is available than on the mesa or even on the adobe soil of the hills, where *Parkinsonia microphylla*, a related species, does well. *Prosopis velutina*, the mesquite, grows chiefly in low ground, within reach of abundant water, but it also occurs, though scattering and undersized, on the adobe soil of rocky hills. Like the *palo verde* and many other leguminous plants, the leaves of the mesquite exhibit in their structure and position excellent adaptations for the prevention of excessive transpiration. *Acacia constricta*, of similar distribution, occurs on the mesa and also on rocky upland. It is a vigorous shrub,

one or two meters in height. These several species of Parkinsonia, Prosopis, and Acacia thrive well under the rather severe conditions to which they have become accustomed; they all retain, however, manifest traces of mesophytic habits, particularly in their choice of habitat.

The species assigned to the third group, among which are *Fouquieria splendens*, *Holacantha Emoryi*, *Koerberlinia spinosa*, and *Zizyphus lycioides*, present more striking modifications of form and structure than do any of the members of the preceding groups, and, though differing greatly among themselves, agree in possessing such conspicuous adaptations to xerophytic conditions as easily to rank next to members of the following biological group.

The cacti are commonly taken to represent the extreme type of xerophytes, but notwithstanding various striking features common to members of this order, there are essential differences of habit and adaptation, even between closely related species, rendering it quite impossible to generalize from the study of "typical forms" in the investigation of biological problems presented by them.

The half-shrubby and herbaceous plants are much like those of other regions, exhibiting as a rule no structures that would be thought of as distinctively xerophytic, but accommodating themselves to desert conditions by their habits, especially such as enable them to take advantage of periods favorable for rapid development and production of seeds.

By way of first ascertaining whether any of the plants of these several groups absorb enough water through their leaves or internodes to be readily detected by weighing, the following method was employed: A small branch with leaves functionally active, though often showing plainly the effects of long drouth, was severed and the cut end immediately covered with vaseline. In a few instances, which are specified, branches without leaves were used. The branch was then weighed and directly afterwards immersed in water, except at the cut end, for a definite time, usually about three hours. At the end of this period, after exposure to the open air long enough to be certain that the surface was fully dry, the branch was again weighed, and the increase of weight, if any, was

taken to represent closely the amount of water absorbed, though, owing to loss during the operation of drying the surface, the amount absorbed must often have been rather greater than the increase of weight indicated. In the first preliminary set of observations, a pair of large balances, weighing satisfactorily to ten milligrams, was employed; but in subsequent experiments quantitative balances were used, the weighing being made to a milligram in each case. Changes during the process of weighing rendered it as useless as it was unnecessary to attempt a higher degree of accuracy.

Inspection of Table I shows that leafy shoots of Celtis, Covillea, and Lycium, by immersion in water for three hours, gained 1.9 to 5 per cent. of their original weight; Atriplex in a little longer

TABLE I.

PRELIMINARY TEST OF CAPACITY FOR ABSORPTION. *November 1904.*

Species	Date	Time	Weight in grams	Gain or loss per cent.
Covillea tridentata (1).....	Nov. 1	10:12 A. M.	18.540	
		1:12 P. M.	19.250	3.8 gain
Covillea tridentata (2)	" 9	10:55 A. M.	8.235	
		1:56 P. M.	8.650	5.0 "
Celtis pallida.....	" 1	10:57 A. M.	24.920	
		1:57 P. M.	26.000	4.3 "
Lycium Berlandieri.....	" 1	10:45 A. M.	7.105	
		1:45 P. M.	7.240	1.9 "
Acacia constricta.....	" 1	11:14 A. M.	6.260	
		1:14 P. M.	6.352	1.5 "
Prosopis velutina.....	" 1	10:30 A. M.	4.200	
		1:30 P. M.	4.250	1.2 "
Parkinsonia microphylla.....	" 1	10:22 A. M.	10.410	
		1:22 P. M.	10.490	0.8 "
Parkinsonia Torreyana.....	" 9	11:03 A. M.	4.070	
		2:02 P. M.	4.085	0.4 "
Atriplex canescens.....	" 17	10:21 A. M.	2.140	
		1:44 P. M.	2.250	5.1 "
Zizyphus lycioides.....	" 9	11:39 A. M.	19.270	
		3:25 P. M.	19.320	0.3 "
Fouquieria splendens.....	" 9	11:21 A. M.	21.770	
		2:24 P. M.	21.920	0.7 "
		3:32 P. M.	21.770	
Koerberlinia spinosa.....	" 10	10:41 A. M.	8.650	
		1:40 P. M.	8.670	0.2 "
Encelia farinosa.....	" 9	12:00 M.	5.010	
		3:00 P. M.	5.320	6.2 "
		3:18 P. M.	5.000	
Sphaeralcea pedata.....	" 9	12:07 P. M.	1.120	
		3:12 P. M.	1.180	5.4 "
		3.21 P. M.	1.110	

period gained 5.1 per cent.; Parkinsonia, Prosopis, and Acacia gained 0.4 to 1.5 per cent.; and Zizyphus, Fouquieria, and Koeberlinia, all without leaves, showed almost no appreciable gain. Species of Sphaeralcea and Encelia gained in weight 5.4 and 6.2 per cent. respectively, but promptly lost all they had gained by a few minutes drying.

It will be noticed that of the plants employed in this preliminary work those without leaves absorbed no water to speak of, while those in leaf fell into two categories, those absorbing and those not absorbing water in quantity. The experiment, therefore, pointed to leaves rather than internodes as agents of absorption, and indicated, apart from Sphaeralcea, Encelia, and the peculiar Atriplex, only the woody species belonging to the first group as likely to prove capable of absorbing much water.

Starting with the suggestions derived from these facts, a more careful and detailed study was undertaken. Cut shoots were still employed for a time, though it was understood that confirmation of results would necessitate the use of entire plants, and these were, as a matter of fact, employed to a large extent in the later work. Care was exercised in the selection of material, and in each case its source and any conditions liable to affect results were noted.

GROUP I.

Celtis pallida.

Four specimens of this species were selected, all in good condition, though apparently not as active physiologically as they would have been earlier in the year. Numbers 1 and 2 were fresh shoots, while numbers 3 and 4 were small branches taken from older bushes. Those numbered 1 and 3 were cut so as to include a large leaf surface as compared with the other two. In every case the cut ends were covered at once with vaseline, and the first weighing was made as soon as practicable after bringing them to the laboratory. They were then wet at frequent intervals for a little more than three hours, and, after drying the surface, were weighed again, after which they were left in the laboratory to dry until the next day, when the same steps were repeated. Finally they were immersed in water over night and again weighed.

TABLE II.

CELTIS PALLIDA. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Period of treatment
1	Dec. 19	10:44 A. M.	1.834		
		1:55 P. M.	1.853	1 gain	After wetting nearly 3 hrs. 11 min.
	20	9:48 A. M.	1.516	18.2 loss	" drying 19 hrs. 53 min.
		2:10 P. M.	1.592	5 gain	" wetting nearly 4 hrs. 22 min.
	21	10:35 A. M.	1.895	19 "	" " " 20 " 25 "
2	19	10:54 A. M.	1.392		
		2:02 P. M.	1.410	1.3 gain	After wetting nearly 3 hrs. 8 min.
	20	9:57 A. M.	1.192	15.5 loss	" drying 19 hrs. 55 min.
		2:25 P. M.	1.238	3.9 gain	" wetting nearly 4 hrs. 28 min.
	21	10:52 A. M.	1.440	16.3 gain	" " " 20 " 27 "
3	19	11:13 A. M.	2.137		
		2:20 P. M.	2.185	2.2 gain	After wetting nearly 3 hrs. 7 min.
	20	10:07 A. M.	1.734	20.6 loss	" drying 19 hrs. 47 min.
		2:38 P. M.	1.870	7.8 gain	" wetting nearly 4 hrs. 31 min.
	21	11:05 A. M.	2.182	16.7 "	" " " 20 " 7 "
4	19	11:25 A. M.	1.505		
		2:31 P. M.	1.521	1.1 gain	After wetting nearly 3 hrs. 6 min.
	20	10:16 A. M.	1.351	11.2 loss	" drying 19 hrs. 45 min.
		2:46 P. M.	1.387	2.7 gain	" wetting nearly 4 hrs. 30 min.
	21	11:15 A. M.	1.535	10.7 "	" " " 20 " 29 "

Inspection of Table II shows:

1. That all four specimens absorbed water very slowly just after they were freshly cut, and that the rate of absorption was greatly increased after they had lost weight by remaining over night in the dry air of the laboratory.

2. The rate of absorption showed a correlation with extent of leaf surface, being considerably greater in the two specimens with large extent of leaf surface than in the other two.

3. The weight lost by drying for a given period was nearly or quite regained when the leaves were given a full supply of water for a corresponding length of time. The capacity of this species for leaf absorption, under the conditions described, is thus fully demonstrated. Its deportment in the seedling stage, which offered for experiment perfectly fresh and unmutilated material, will next be considered.

Seedlings of *Celtis pallida* were grown from seeds sown November 14, 1904. When used for experiment in January and February,

1905, they were all in healthy condition, and when taken up were found to have fine vigorous roots. In addition to the cotyledons, which were still capable of photosynthesis, each seedling had two or three perfectly healthy green leaves that had attained the length of about one centimeter. The seedlings were transplanted into earth contained in glass vials of convenient size for accurate weighing, sheet rubber being used to prevent evaporation from the soil.

In the case of seedling number 1 the earth was very moist when the rubber was adjusted, and it was found that this plant, which was transpiring vigorously, showed almost no capacity for absorption. The case was different with seedling number 2, which was left some five days after transplanting with the soil open to the air, so that it became relatively dry before the rubber was adjusted. The cotyledons of number 1 were removed, their place of attachment being carefully covered with vaseline; number 2 had one large cotyledon which remained in place during the experiment. These details are necessary to an understanding of the different behavior of the two seedlings as shown by Tables III and IV, which cover the period from January 21 to February 1, at which latter date the experiment was concluded.

It is seen that both seedlings transpired regularly and largely, but that number 1, in spite of the fact that its transpiring surface had been lessened by the loss of its cotyledons, exhibited a decidedly higher rate of transpiration than number 2, which was in drier

TABLE III.

CELTIS PALLIDA. SEEDLING NO. 1. *January 1905.*

Date	Time	Weight in grams	Loss or gain	Conditions
Jan. 21	1:19 P. M.	26.256		
	4:05	26.229	0.027 loss	After standing in dry air
23	10:15 A. M.	26.094	0.135 "	" " " " "
	2:50 P. M.	26.061	0.033 "	" " " " "
25	10:50 A. M.	25.936	0.125 "	" " " " "
26	9.50	25.870	0.066 "	" " " " "
27	9:28	25.806	0.064 "	" " " " "
	2:53 P. M.	25.810	0.004 gain	After wetting
	3:41	25.803	0.007 loss	" standing in dry air
28	11:02 A. M.	25.762	0.041 "	" " " " "
	1:33 P. M.	25.764	0.002 gain	" wetting
	2:58	25.759	0.005 loss	" standing in dry air

TABLE IV.

CELTIS PALLIDA. SEEDLING NO. 2. *January and February 1905.*

Date	Time	Weight in grams	Loss or gain	Conditions
Jan. 30	10:09 A. M.	22.638		
	1:10 P. M.	22.630	0.008 loss	After standing in dry air
	3:40	22.626	0.004 "	" " " " "
31	9:45 A. M.	22.653	0.027 gain	" wetting
	12:45 P. M.	22.628	0.025 loss	" standing in dry air
	3:13	22.634	0.006 gain	" wetting
Feb. 1	9:48 A. M.	22.592	0.042 loss	" standing in dry air
	9:50	0.027		Weight of plant above ground
	2:08 P. M.	0.045	0.028 gain	After wetting

soil, an interesting result in harmony with earlier experiments, showing the direct relation between available soil water and rate of transpiration.[3]

On the other hand, while the quantity of water absorbed by number 1 was so meager as to be negligible, that absorbed by number 2 was much more, in one case almost exactly 100 per cent. of its own weight, i. e., of the part above ground when it was afterwards severed from the root. Number 2, although apparently perfectly healthy while the work was in progress, seems nevertheless to have reached a condition in which the diminished supply of water from the soil was followed by a marked acceleration of leaf absorption, while in the case of number 1, growing as it was in moist soil, no such compensation was made or required.

Of interest as bearing on the validity of determinations of absorption by the use of detached shoots is the fact that while seedling number 2, after it had finally been cut off at the surface of the ground, absorbed in a few hours its own weight of water, it had done precisely the same thing before mutilation, only in longer time. It may well be that a detached shoot, cut off from its normal source of water supply, will absorb more rapidly through its leaves than the same shoot, which, while attached, is supplied, even inadequately, from the soil; but this difference plainly does not justify the degree of discredit that has been thrown upon evidence derived from experiments with separated parts of plants.

Three other seedlings of *Celtis pallida* were treated like the preceding ones, except that the observations were not begun until

[3] SPALDING, V. M., Soil water in relation to transpiration. Torreya **5**:25. 1905.

the plants had been some weeks in the vials to which they were transplanted, and weighings were made during a longer period and with more complete records as to soil conditions, health of seedling, etc. Their records as to weight are given in Tables V, VI, and VII. All of these seedlings were in a healthy condition and apparently capable of entirely normal development. The small extent of surface through which absorption and transpiration took place renders the consistency of the results all the more striking. In every case water was absorbed when it was presented to the leaves and internodes, and transpiration was resumed as soon as their surfaces were dried.

TABLE V.

CELTIS PALLIDA. SEEDLING NO. 3. *February 1905.*

Date	Time	Weight in grams	Loss or gain	Conditions
Feb. 14	11:20 A. M.	23.084		Weight of seedling and outfit
	2:25 P. M.	23.091	0.007 gain	After immersion in rain water
15	9:40 A. M.	23.044	0.047 loss	" standing in dry air
	11:55	23.053	0.009 gain	" immersion in rain water
16	11:42 A. M.	23.007	0.046 loss	" standing in dry air
17	2:11 P. M.	23.046	0.039 gain	" immersion in rain water
20	10:23 A. M.	22.895	0.151 loss	" standing in dry air
	2:51 P. M.	22.916	0.021 gain	" immersion in rain water
21	10:28 A. M.	22.932	0.016 "	" " " " "
	12:00 M.	22.907	0.025 loss	" standing in dry air
	3:02 P. M.	22.887	0.020 "	" " " " "
22	12:08	22.835	0.052 "	" " " " "
	12:11	22.828		Weight after removing cotyledon
	2:14	22.835	0.007 gain	After immersing in rain water
	2:34	0.035		Weight when cut at surface of earth
	2:38	22.799		" of vial, rubber, and earth
25	1:58	0.015		" of plant above ground, air-dried in laboratory

When the first weighing was made, February 14, seedling no. 3 had two cotyledons, still attached, and three foliage leaves. The cotyledons showed some indications of drying. The earth in the glass vial in which the seedling was growing was becoming rather dry, but still contained sufficient water to maintain a transpiration current for a week and probably longer. On February 16, the note was made "one of the cotyledons drying, curled, and getting stiff; the other paler than the foliage leaves, but still flexible, otherwise the seedling is in good condition."

On February 22 the cotyledons were removed and the subse-

quent deportment of the seedling indicates that their failing condition previous to removal may be disregarded as not materially affecting the results. As the table shows, the weight of the whole plant above ground, including cotyledons, was less than the weight of water transpired in 19 hours (Feb. 14–15) and also less than the gain of weight by absorption in 26 hours (Feb. 16–17), a conclusive proof of the relatively large quantities of water absorbed and transpired by this seedling during the period of experimentation. The facts regarding seedlings 4 and 5 are so fully set forth in Tables VI and VII as to render further explanation unnecessary.

TABLE VI.

CELTIS PALLIDA. SEEDLING NO. 4. *February and March 1905.*

Date	Time	Weight in grams	Loss or gain	Conditions
Feb. 14	3:30 P. M.	20.130		Weight of plant and outfit
15	10:02 A. M.	20.090	0.040 loss	After standing in dry air
	12:47 P. M.	20.093	0.003 gain	" immersion in rain water
16	12:00 M.	20.031	0.062 loss	" standing in dry air
17	3:11 P. M.	20.051	0.020 gain	" immersion in rain water
20	10:46 A. M.	19.821	0.230 loss	" standing in dry air
	3:19 P. M.	19.825	0.004 gain	" immersion in rain water
21	10:54 A. M.	19.830	0.005 "	" " " " "
	12:11 P. M.	19.813	0.017 loss	" standing in dry air
22	12:29	19.696	0.117 "	" " " " "
	3:08	19.707	0.011 gain	" immersion in rain water
March 2	10:04 A.M	19.080	0.627 loss	" standing in dry air
	2:04 P. M.	19.085	0.005 gain	" immersion in rain water
	2:25	19.080	0.005 loss	" standing in dry air
	2:30	0.070		Weight when cut off at surface of earth

TABLE VII.

CELTIS PALLIDA. SEEDLING NO. 5. *February 1905.*

Date	Time	Weight in grams	Loss or gain	Conditions
Feb. 20	11:16 A. M.	20.207		Weight of plant and outfit
	3:28 P. M.	20.204	0.003 loss	After wetting with rain water (not immersing)
21	11:09 A. M.	20.219	0.015 gain	After immersion in rain water
	12:15 P. M.	20.214	0.005 loss	" standing in dry air
22	12:34	20.172	0.042 "	" " " " "
	3:18	20.178	0.006 gain	" immersion in rain water
	3:33	0.025		Weight when cut off at surface of earth
25	2:11	0.012		Weight after air drying

Covillea tridentata.

The specimens of creosote bush selected for experiment were taken from four different sources, for the sake of securing material as different as practicable in regard to the amount of water in the tissues. Number 1 was from a bush growing near an irrigating ditch, where it had been abundantly supplied with water. Its leaves were large, dark green, and fresh, and numerous flower buds had been formed. Number 2 was from a plant growing on the mesa a few rods distant. Its leaves were smaller and lighter green, and in comparison with number 1 it was plainly a dry ground form, though it did not have the appearance of having suffered to any great extent from lack of water. Numbers 3 and 4 were from plants growing on the mesa, near the foot of the laboratory hill, where in a dry time the Covillea, the only shrub that keeps alive there, shows the effects of drouth very badly. Their leaves were still smaller and paler in color, those of number 4 especially, indicating by their minute size and other peculiarities a plant that had long lacked a sufficient supply of water. The contrast between this and the first member of the series was very striking. It should be stated, however, that none of the specimens were in quite so dried-up a condition as those employed early in November before the December rains, which though meager—0.82 inch (21^{mm}) thus far—had freshened vegetation to some extent. The dried-up leaves that were dying in November had been shed, and the leaves remaining on the bushes when the experiment was conducted, late in December, were apparently in a vitally active condition.

It will be noticed by reference to Table VIII that, precisely as in the case of Celtis, all the specimens of Covillea gained very little in weight as the result of wetting soon after they were cut. Number 1, from the irrigated bush, gained least, and number 4, from the dry ground plant, gained most. After prolonged drying and again wetting, the gain was much greater than before, the greater gain in each case being made by number 4, which, as already stated, was from the most distinctively dry ground form.

The deportment of number 1, from the robust, well-watered bush, is instructive, especially as it may throw light on the question as to whether leaf absorption is a normal process that takes place

TABLE VIII.

COVILLEA TRIDENTATA. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Period of treatment
1	Dec. 26	11:05 A. M.	2.529		
		2:17 P. M.	2.538	0.4 gain	After wetting nearly 3 hrs. 12 min.
	28	10:32 A. M.	1.957	22.9 loss	" drying 44 hrs. 15 min.
		2:18 P. M.	1.996	2.0 gain	" wetting nearly 3 hrs. 46 min.
	29	10:50 A. M.	2.188	9.6 "	" " " 20 " 32 "
2	26	11:12 A. M.	2.434		
		2:35 P. M.	2.453	0.8 gain	After wetting nearly 3 hrs. 23 min.
	28	10:40 A. M.	2.234	8.9 loss	" drying 44 hrs. 05 min.
		2:33 P. M.	2.258	1.1 gain	" wetting nearly 3 hrs. 53 min.
	29	11:03 A. M.	2.416	7.0 "	" " " 20 " 30 "
3	26	11:21 A. M.	2.261		
		2:58 P. M.	2.281	0.8 gain	After wetting nearly 3 hrs. 37 min.
	28	10:48 A. M.	1.980	13.2 loss	" drying 43 hrs. 50 min.
		2:45 P. M.	2.020	2.0 gain	" wetting nearly 3 hrs. 57 min.
	29	11:14 A. M.	2.225	10.1 "	" " " 20 " 29 "
4	26	11:28 A. M.	2.646		
		3:03 P. M.	2.688	1.6 gain	After wetting nearly 3 hrs. 35 min.
	28	10:55 A. M.	2.357	12.3 loss	" drying 43 hrs. 52 min.
		2:56 P. M.	2.415	2.5 gain	" wetting nearly 4 hrs. 1 min.
	29	11:23 A. M.	2.766	14.5 "	" " " 20 " 27 "

under natural conditions. This shoot, with its large, fresh, turgid leaves, lost water by drying approximately twice as rapidly as did those from dry ground, with their much smaller leaves and firmer tissues, and on subsequent wetting absorbed far less than the latter in proportion to previous loss. Unlike these, moreover, the leaves of the first specimen, in the course of alternate drying and wetting, lost their fresh look and became discolored. The impression was received that this specimen, taken from a perfectly fresh plant and requiring no additional supply of water, suffered pathological changes in the course of the treatment to which it was subjected, while the others, coming from dry ground plants in need of water, absorbed it as by a perfectly normal process. Even these, however, were not in a condition for rapid leaf absorption when first cut, their gain per cent. being decidedly less for a given period than that exhibited by individuals of the same species during observations made before the December rains. In brief, the experiments of December 26–29, in connection with those of November 1–9, indicate on the part of the creosote bush marked capacity for

subaerial absorption after protracted drouth, but more limited capacity for such absorption, even if artificial drying is resorted to, when it is receiving a better supply of water.

Lycium Berlandieri.

At the time when the observations on Lycium were made, late in December, most of the summer leaves had fallen and fresh ones, following recent light rains, were only beginning to appear. Consequently it was difficult to secure entirely satisfactory material, but a few specimens were finally obtained for experiment which were in a normal and active condition. The leaves of this species are small, only about one centimeter in length, but otherwise the plant gives the impression, as already stated, of having retained up to the present time distinctively mesophytic tendencies. The rapidity with which the leaves were transpiring was at once obvious when weighing was undertaken, and, as in cases previously cited, absorption was found to take place extremely slowly while the leaves were still fresh. Even after drying, water was absorbed in no case as rapidly as it had been lost. Thus number 2 lost 3 per cent. of its weight by drying three and one-half hours, and gained afterwards by wetting nearly four hours 1.9 per cent. Of the actual capacity of this species for subaerial absorption the experiments leave no room for doubt; but the specimens employed deported themselves much like the well-watered Covillea, except that no suggestion of pathological change in the course of the treatment to which they were subjected was noted. When gathered they were simply in the condition of fresh, actively transpiring plants,

TABLE IX.

LYCIUM BERLANDIERI. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Period of treatment
1	Dec. 28	10:15 A. M.	3.065		
		1:47 P. M.	3.076	0.4 gain	After wetting nearly 3 hrs. 32 min.
	29	10:15 A. M.	3.235	5.2 "	" " nearly 20 hrs. 28 min.
		1:42 P. M.	2.956	8.7 loss	" drying 3 hrs. 27 min.
		3:25	3.002	1.6 gain	" wetting nearly 1 hr. 43 min.
2	28	10:22 A. M.	3.122		
		1:56 P. M.	3.028	3.0 loss	After drying 3 hrs. 34 min.
	29	10:00 A. M.	2.802	7.5 "	" " 20 " 04 "
		1:53 P. M.	2.855	1.9 gain	" wetting nearly 3 hrs. 53 min.

which apparently could derive no advantage from an additional supply of water presented to their leaves.

The record of these three species of Celtis, Covillea, and Lycium has been given at length, on account of the importance of establishing beyond doubt the fact that in these plants, which have been taken to represent desert species that retain in structure and habits obvious indications of mesophytic origin, leaf absorption certainly takes place, and apparently as an entirely normal process. We have next to deal with a group of species genetically related, which deport themselves quite differently from members of the first biological group in regard to leaf absorption. As representatives of this second group, species of Parkinsonia, Prosopis, and Acacia were selected, all belonging to the Leguminosae. The record of experiments and their results is such as to admit of statement in few words.

GROUP II.

Parkinsonia Torreyana.

The specimens of *palo verde* employed in this work were seedlings some two months old. One was cut about thirteen hours, the other (number 2) an hour and a half before weighing. After weighing an attempt was made to wet the leaves by repeatedly immersing the seedlings in water. The experiment might fairly have been dropped at this point, since, as it was found impossible to wet them, leaf absorption could hardly be thought of; but as there remained a possibility of some slight absorption where drops of water collected on the surface of the youngest parts, the attempt was continued with number 1, which was repeatedly immersed during a period of something over three hours.

As seen from Table X this seedling, so far from gaining by absorption of water presented to it, actually lost 1.8 per cent. of its weight in three hours and thirteen minutes, its surface having remained almost entirely unwetted, so that loss of water was possible during the whole, or nearly the whole, of this period. Seedling number 2 was allowed to dry, after an unsuccessful series of attempts to wet its surface. Its loss of weight, as might be expected, was greater than that of number 1.

If these results are compared with those of November 1 and 9, derived from similar experiments with shoots of *Parkinsonia micro-*

TABLE X.

PARKINSONIA TORREYANA. SEEDLINGS. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Conditions
1	Dec. 31	9:32 A. M.	0.961		
		12:45 P. M.	0.944	1.8 loss	After repeatedly immersing in water
2		9.37 A. M.	0.886		After drying, following repeated attempts to wet the surface
		12:52 P. M.	0.855	3.5 loss	

phylla and *P. Torreyana*, the conclusion must be drawn that the species of Parkinsonia represented here either absorb no water, or at most an exceedingly small quantity, through their leaves. Before making the experimental test it was thought that the fresh, rapidly transpiring leaves of seedlings might exhibit a capacity for absorption not shown by those of older plants, but this has not proven to be the case.

Prosopis velutina.

Work on the mesquite was carried on at intervals for a number of weeks in January, February, and March, the material first employed being obtained from mature specimens, while in the later experiments seedlings were used. Of specimens taken from mature plants only the leaves were immersed in water. In some cases the upper surface resisted wetting, while in others both surfaces were easily wetted. This was followed, as indicated by some increase of weight, by absorption of water in limited quantities. The seedlings which were employed in subsequent experiments remained unwetted in all cases when they were immersed in water, and in spite of the fact that two of the specimens had been left to dry as much as forty-two hours and showed the effects of this treatment before immersion, there is no evidence that they absorbed any water whatever.

It is apparent, then, that as long as the leaves of the mesquite are perfect and resist wetting they absorb no water, even after drying for some time, but that they may absorb more or less after they have become old and can be wetted. It is very questionable, to say the least, whether in the latter case this process has any physiological significance. It would seem that in the mesquite, as in the *palo verde*, adaptations to xerophytic conditions have been carried so far in the direction of preventing excessive transpiration that leaf absorption, as a normal process, does not take place.

Acacia constricta.

A series of experiments with this species was carried out, but it was found unfavorable for exact results, owing in part to the fact that its leaflets become tightly closed after wetting, thus rendering it difficult to secure perfect drying of the surface without overexposure and consequent uncertainty as to the true weight. Accordingly, the conviction that the data obtained were unreliable led to their rejection. For this second group, therefore, we are restricted to the positive results obtained from Parkinsonia and Prosopis, which exhibit either no capacity or very slight capacity for leaf absorption, so long as the leaves are in perfect condition and normally active.

GROUP III.

This third group includes representatives of a number of genera much modified in form and structure, and differing among themselves in their methods of meeting desert conditions. Several of these are more commonly seen without than with leaves, photosynthesis then taking place in their green shoots; while others, more dependent on leaf activity, are commonly in a leafless condition during a large part of the year, pushing out new leaves promptly when conditions are favorable, and dropping them again when they become adverse, as is seen particularly in the case of Fouquieria.

Holacantha Emoryi.

Of this peculiar shrub a small branch with leaves was cut and left several hours to dry. At the end of this time it was still fresh, with no indication of wilting. After weighing it was wet for two hours and thirty-nine minutes, after which it was weighed again, the weight remaining unchanged. Leaving the shoot now to dry until the next day, and then wetting it for four hours and twelve minutes, there was a gain in weight of only 0.5 per cent. Part of the same shoot, destitute of leaves, was treated in the same way, and, after wetting four hours and eleven minutes, also showed a gain of barely 0.5 per cent. of its former weight. These results indicate on the part of this species capacity for leaf absorption so inconsiderable that it may be neglected.

Koerberlinia spinosa, a closely related species, agrees with Holacantha as far as observations have yet been made. Only leafless

branches have been obtainable, but these, as in the preceding species, are green, and for a large part of the year the plant has no other organ of photosynthesis. So far, then, as present evidence goes, absorption through leaves or internodes is not to be predicated of either of these plants.

Zizyphus lycioides.

After the preliminary experiments already recorded, very little satisfactory material for the study of this species was obtainable, as the plant cast its leaves and remained bare until after the period of study was concluded. From observations made early in the year, however, it appears that leafless shoots of Zizyphus do not absorb water in appreciable quantity, but that leafy shoots have considerable absorptive capacity, indicating that it is the leaves and not the internodes through which absorption takes place.

Fouquieria splendens.

Leafy shoots of the *ocotillo*, as shown by Table XI, absorb considerable water when wet for some time after drying. As in various other cases, the loss of weight on drying the shoots after wetting is considerably more rapid than the preceding gain by absorption.

TABLE XI.

FOUQUIERIA SPLENDENS. *January 1905.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Conditions
1	Jan. 26	12:00 M.	1.614		In each case loss followed drying and gain followed wetting the sp-eci mens during the periods indicated in the time column.
	27	10:00 A. M.	1.582	1.9 loss	
	28	11:40	1.664	5.2 gain	
		3:20 P. M.	1.598	4.0 loss	
	30	1:02	1.518	5.0 "	
		3:28	1.530	0.8 gain	
		4:09	1.523	0.5 loss	
	31	4:15	1.490		
	Feb. 1	1:32	1.585		
2	Jan. 26	2:31 P. M.	4.214		
	27	10:15 A. M.	4.112	2.4 loss	
	28	11:45	4.059	1.3 loss	
	30	2:04 P. M.	4.363	7.5 gain	
		3:04	4.255	2.5 loss	
		4:02	4.197	1.4 "	
	31	11:42 A. M.	3.761	10.0 "	
		2:45 P. M.	3.840	2.1 gain	
		3:45	3.798	1.1 loss	

It appears, then, that for this biological group, which includes a number of plants for the most part unrelated systematically, no general rule can be formulated regarding leaf absorption. The experiments go to show that Holacantha and Koerberlinia hardly absorb at all, while Fouquieria is certainly capable of absorbing considerable quantities of water.

GROUP IV.

The only representatives of the cacti that have been studied thus far are two species of Opuntia, *O. Engelmanni* and *O. versicolor*. A number of specimens of each species were selected after a prolonged drouth, the results of which were plainly seen in their much shrunken condition, very favorable, it would seem, for the demonstration of absorption if this ever takes place. As the material was rather bulky the large balances were employed, a terminal joint in each case being severed and weighed; but there is no reason to doubt the substantial accuracy of the results.

As shown by Tables XII and XIII, *Opuntia Engelmanni* did not in any case gain more than 0.6 per cent. of its original weight, even when immersed in water upwards of 45 hours, and it is safe to conclude from this result, drawn from experiments with a number of specimens, that the species in question does not normally absorb any considerable quantity of water in this way. *Opuntia versicolor*, on the other hand, treated in the same manner, showed

TABLE XII.

OPUNTIA ENGELMANNI. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Conditions
1	Dec. 3	10:15 A. M.	82.360		In each case gain followed wetting and loss followed drying during the periods indicated in the time column.
		1:30 P. M.	82.850	0.6 gain	
	5	11:00 A. M.	83.360	0.6 "	
2	6	10:12 A. M.	72.085		
		1:10 P. M.	72.470	0.5 gain	
		3:05	72.080	0.5 loss	
3		10:39 A. M.	131.750		
		1:33 P. M.	132.290	0.4 gain	
		3:20	131.760	0.4 loss	

TABLE XIII.

OPUNTIA VERSICOLOR. *December 1904.*

No.	Date	Time	Weight in grams	Loss or gain per cent.	Conditions
1	Dec. 3	10:30 A. M.	16.390		
		1:55 P. M.	16.770	2.3 gain	See Table XII
	5	11:11 A. M.	16.780	0.1 "	
2	6	9:55 A. M.	10.640		
		12:14 P. M.	10.850	2.0 gain	
		3:02	10:630	2.0 loss	
3		10:30 A. M.	8.115		
		12:35 P. M.	8.360	3.0 gain	
		3:10	8.115	2.9 loss	

a gain of 2 to 3 per cent. The specimens most shrunken with drouth were found to absorb water most rapidly.

The rapid loss of water and the curiously close correspondence in each case between the percentages of gain and loss, suggest that in this species it is merely the tubercles that act as organs of absorption, and notwithstanding the fact that the water absorbed is so promptly given off in a dry atmosphere, it appears probable that in a period of frequent light rains the continued absorption of water by the tubercles is precisely the necessary preparation for the development of the young shoot which presently follows. Meantime the different deportment of these two species of Opuntia as regards amounts of water absorbed, corresponding as it does with a marked difference in size of their tubercles, suggests the desirability of a more extended comparison of these structures in different cacti with reference to their capacity for absorption and the physiological value of the process.

GROUP V.

A discussion of the annuals and partly herbaceous perennials that have been referred to a fifth biological group, many of which, structurally at least, are not to be thought of as characteristic desert plants, does not fall within the limits of the present study. As already stated, as many of them as have been studied agree in promptly absorbing water when it is presented to their leaves and internodes, which, however, is given off so rapidly in dry air that it hardly seems possible that its absorption is of any utility. *Cf.* Table I, Encelia and Sphaeralcea.

SUMMARY.

From the preceding observations and experiments, in which woody plants were chiefly employed, it has been seen that certain species of desert plants of southern Arizona absorb water presented to their leaves and internodes, while others do not. The species represented in the vicinity of the Desert Botanical Laboratory may be divided into several biological groups, based primarily on the water relation, of which leaf absorption is a phase. Thus, in the first group, including shrubs, which retain well marked mesophytic tendencies, leaf absorption is characteristic. Members of the second group, more distinctively xerophytic in various structural particulars, are incapable of leaf absorption during their period of normal activity. The third group, decidedly xerophytic, but including species of widely different structure and habits, exhibits corresponding differences in regard to subaerial absorption, which takes place in some of its representatives and not in others. The fourth group, including cacti which are assumed to represent the extreme type of xerophytes, also exhibits interesting differences in size and structure of the tubercles by means of which water is absorbed. Finally, members of a provisional fifth group, which in habit and structure are nearer than any other others to the mesophytes of moist temperate regions, absorb water largely, but very quickly give it up again.

It may be doubted, perhaps, whether this classification, based on biological relations, has in itself any permanent value, but meantime it serves to express and emphasize what is apparently no mere theoretical conception, but a simple historical fact, namely, that differences of habit on the part of these desert plants, as well as the structural adaptations with which they are correlated, have become established step by step together, during the long period of geographical changes through which the land they now occupy has been passing. A discussion of the physiological significance of the facts which have been brought out does not fall within the province of this paper.

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